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Assessing vegetation structure and ANPP dynamics in a grassland-shrubland Chihuahuan ecotone using NDVI-rainfall relationships

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Abstract

Climate change and the widespread alteration of natural habitats are major drivers of vegetation change in drylands. A classic case of vegetation change is the shrub-encroachment process that has been taking place over the last 150 years in the Chihuahuan Desert, where large areas of grasslands dominated by perennial grass species (black grama, *Bouteloua eriopoda*, and blue grama, *B. gracilis*) have transitioned to shrublands dominated by woody species (creosotebush, *Larrea tridentata*, and mesquite, *Prosopis glandulosa*), accompanied by accelerated water and wind erosion. Multiple mechanisms drive the shrub-encroachment process, including exogenous triggering factors such as precipitation variations and land-use change, and endogenous amplifying mechanisms brought about by soil erosion-vegetation feedbacks. In this study, simulations of plant biomass dynamics with a simple modelling framework indicate that herbaceous (grasses and forbs) and shrub vegetation in drylands have different responses to antecedent precipitation due to functional differences in plant growth and water-use patterns, and therefore shrub encroachment may be reflected in the analysis of landscape-scale vegetation–rainfall relationships. We analyze the structure and dynamics of vegetation at an 18 km² grassland-shrubland ecotone in the northern edge of the Chihuahuan Desert (McKenzie Flats, Sevilleta National Wildlife Refuge, NM, USA) by investigating the relationship between decade-scale (2000–2013) records of medium-resolution remote sensing of vegetation greenness (MODIS NDVI) and precipitation. Spatial evaluation of NDVI-rainfall relationship at the studied ecotone indicates that herbaceous vegetation shows quick growth pulses associated with short-term (previous 2 months) precipitation, while shrubs show a slow response to medium-term (previous 5 months) precipitation. We use these relationships to (a) classify landscape types as a function of the spatial distribution of dominant vegetation, and to (b) decompose the NDVI signal into partial primary production components for herbaceous vegetation and shrubs across the study site. We further apply remote-sensed annual net primary production (ANPP) estimations and landscape type

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classification to explore the influence of inter-annual variations in seasonal precipitation on the production of herbaceous and shrub vegetation. Our results suggest that changes in the amount and temporal pattern of precipitation comprising reductions in monsoonal summer rainfall and/or increases in winter precipitation may enhance the shrub-encroachment process in desert grasslands of the American Southwest.

1 Introduction

Land degradation is pervasive across many dryland regions, which cover over 40 % of the Earth's surface and account for about 30 % of global terrestrial net primary productivity, globally supporting about 2.5 billion inhabitants (Millennium Ecosystem Assessment, 2005). Causes for concern have increased during the last decades due to growing human and climatic pressures in these dryland regions. The most dramatic landscape alterations are those associated with desertification, which are perceived as catastrophic and largely irreversible changes that can ultimately lead to relatively barren ecosystem states (Schlesinger et al., 1990; Okin et al., 2009). A common form of vegetation change in drylands involves the encroachment of desert shrub species into arid and semi-arid grasslands, which has already affected more than 250 million hectares worldwide throughout the US, South America, Southern Africa and Australia (D'Odorico et al., 2012; Turnbull et al., 2014).

A classic case of largely irreversible vegetation shift is the shrub-encroachment process that has been taking place over the last 150 years in the Chihuahuan Desert in south-western USA and northern Mexico, where large areas of grasslands dominated by C_4 perennial grass species (black grama, *Bouteloua eriopoda*, and blue grama, *B. gracilis*) have been replaced by shrublands dominated by C_3 desert shrub species (mainly creosotebush, *Larrea tridentata*, and honey mesquite, *Prosopis glandulosa*), accompanied by accelerated water and wind erosion (for example, Schlesinger et al., 1990; Wainwright et al., 2000; Mueller et al., 2007; Ravi et al., 2010). A complex range of mechanisms have been suggested to explain the occurrence of this phenomenon,

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including the incidence of external factors that initiate the ecosystem transition, and endogenous amplifying mechanisms of vegetation change brought about by soil erosion-vegetation feedbacks (Turnbull et al., 2012). Long-term records suggest that the current grassland-shrubland transition in the Chihuahuan Desert started with the introduction of large numbers of domestic grazers, which may have facilitated the propagation of desert shrub species by creating gaps of bare soil that favored the establishment of pioneer shrubs (Buffington and Herbel, 1965; van Auken, 2000; Webb et al., 2003). Grazing is also likely to have contributed to reduced shrub mortality by altering the frequency and intensity of natural wildfires (D'Odorico et al., 2012). Changing precipitation amount and distribution has also been invoked as one of the major external drivers of shrub encroachment, which may contribute to vegetation change by shifting competitive plant physiological advantages of grass and desert shrub species (Gao and Reynolds, 2003; Snyder and Tartowsky, 2006; Throop et al., 2012). However, there remains a lack of consensus regarding changes in precipitation in the southwest USA over recent decades. Whilst Petrie et al. (2014) found no significant changes in precipitation in at the Sevilleta Long Term Ecological Research Site in central New Mexico, other studies have reported significant increases in both annual and winter precipitation at the Jornada Experimental Range in southern New Mexico, but concurrent decreases in the size of discrete precipitation events (Wainwright, 2006; Turnbull et al., 2013). Once the shrub-encroachment phenomenon is initiated, the process is further amplified by internal soil erosion-vegetation feedbacks. These internal feedbacks strongly alter the organization and distribution of both vegetation and soil resources (i.e. substrate, soil moisture and nutrients), strengthening the vegetation-change process (Okin et al., 2009; Turnbull et al., 2010a, 2012; Stewart et al., 2014).

Comprehensive understanding of how desert grasslands are responding to the present variability on both climate and land use is critical for environmental management, especially in consideration of uncertainty regarding future climate change across many dryland regions. Remote sensing of vegetation provides a very valuable source of information for landscape monitoring and forecasting of vegetation change in dry-

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lands (Okin and Roberts, 2004; Moreno-de las Heras et al., 2012). Satellite-derived chlorophyll-sensitive vegetation indices, such as the Normalized Difference Vegetation Index (NDVI), provide important information on vegetation structure (e.g. surface cover, aboveground green biomass, vegetation type) and dynamics (Anderson et al., 1993; Peters et al., 1997; Pettorelli et al., 2005; Choler et al., 2010). Multi-temporal series of coarse- and medium-resolution NDVI, now routinely and freely available from several satellite-borne sensors (e.g. the Advanced Very High Resolution Radiometer, NOAA-AVHRR, the Moderate Resolution Imaging Spectro-radiometer, MODIS), offer powerful tools for the analysis of the impacts of environmental change on the distribution and dynamics of arid and semi-arid vegetation (Huete et al., 2002; Holm et al., 2003; Weiss et al., 2004; Pennington and Collins, 2007; Forzieri et al., 2011).

In drylands, where vegetation dynamics are particularly well coupled with rainfall pattern, the relationship between time series of NDVI and precipitation provides specific information on the use of water for the production and maintenance of plant biomass (Pennington and Collins, 2007; Notaro et al., 2010; Veron and Paruelo, 2010). Investigations of the relationships between NDVI and rainfall suggest that arid and semi-arid vegetation responds to antecedent (or preceding cumulative) precipitation rather than to immediate rainfall, since plant growth is affected by the history of available soil moisture (Al-Bakri and Suleiman, 2004; Schwinning and Sala, 2004; Evans and Geerken, 2004; Moreno-de las Heras et al., 2012). The length (or number of days) of antecedent rainfall that best explains the NDVI dynamics of dryland vegetation (hereafter NDVI-rainfall signature of vegetation) appears to be site-specific and strongly dependent on vegetation type (Evans and Geerken, 2004; Prasad et al., 2007; Garcia et al., 2010). Herbaceous vegetation (i.e. grass and forb life-forms) and shrubs usually show important differences in the patterns of vegetation growth and water-use, which mediate the responses of plant biomass to rainfall in drylands (Ogle and Reynolds, 2004; Gilad et al., 2007; Pennington and Collins, 2007; Forzieri et al., 2011; Stewart et al., 2014). Thus, the study of the relationship between the NDVI and precipitation may offer impor-

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tant clues for detecting broad-scale landscape changes involving grassland-shrubland transitions in arid and semi-arid landscapes, resulting from environmental change.

The aim of this study is to analyze landscape dynamics at a Chihuahuan grassland-shrubland ecotone (McKenzie Flats, Sevilleta National Wildlife Refuge, New Mexico, USA) by studying the relationship between decade-scale (2000–2013) records of remote-sensed vegetation greenness (MODIS NDVI) and precipitation. Our analysis is based on a new approach that examines characteristic NDVI-rainfall relationships for dominant vegetation types (i.e. herbaceous vegetation and woody shrubs) to investigate the organization and dynamics of vegetation as a way of evaluating how the shrub-encroachment process occurs.

This paper is organized in two parts. First, we use a simple, process-based model to illustrate the conceptual underpinning and theoretical basis of our study: the biophysical control of the relationship between plant biomass dynamics and antecedent precipitation for dryland herbaceous and shrub vegetation. Secondly, we empirically define reference NDVI-rainfall signatures of herbaceous and shrub vegetation for a broad 18 km² Chihuahuan ecotone, and further use these vegetation-type specific relationships between vegetation greenness and antecedent precipitation: (i) to analyze the spatial organization and dynamics of net primary production (NPP) for herbaceous vegetation and shrubs, and (ii) to explore the impact of inter-annual variations in seasonal precipitation on the dynamics of vegetation production at the grassland-shrubland ecotone.

2 Theoretical basis: herbaceous and shrub plant biomass–rainfall relationships

Dryland herbaceous vegetation (i.e. grass and forb life-forms) and shrubs usually exhibit important differences in the patterns of vegetation growth and water-use. Herbaceous vegetation typically shows quick and intense growth pulses synchronized with major precipitation events, while the dynamics of plant biomass for shrubs is generally less variable in time (Sparrow et al., 1997; Lu et al., 2003; Garcia et al., 2010). These

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dissimilar growth responses are controlled biophysically by the different plant growth and mortality rates associated with herbaceous vegetation and shrubs. While grasses and forbs are associated with high rates of plant growth and mortality, shrubs are associated with low plant growth and mortality rates (Ogle and Reynolds, 2004; Gilad et al., 2007).

We use a simplified version of the dynamic model developed by Rietkerk et al. (2002) to illustrate conceptually how the vegetation-specific rates of plant growth and mortality control the relationship between the dynamics of aboveground biomass and precipitation for herbaceous vegetation and shrubs in drylands. The model consists of two inter-related differential equations; one describing the dynamics of vegetation (aboveground plant biomass, B , g m^{-2}) and the other describing soil-moisture dynamics (soil-water availability, W , mm).

Changes in plant biomass are controlled by plant growth and mortality:

$$\frac{dB}{dt} = g_{\max} \frac{W - W_0}{W + k_w} B - mB, \quad (1)$$

where plant growth is a saturation function of soil-moisture availability, and is determined by the maximum specific plant-growth rate (g_{\max} , day^{-1}), the permanent wilting point or minimum availability of soil moisture for vegetation growth (W_0 , mm), and a half saturation constant (k_w , mm). Plant senescence (biomass loss) is controlled by a plant-specific mortality coefficient (m , day^{-1}).

Soil-water dynamics are controlled by rainfall infiltration, plant transpiration, and soil moisture loss due to both deep drainage and direct evaporation:

$$\frac{dW}{dt} = P \frac{B + k_i \cdot i_0}{B + k_i} - c g_{\max} \frac{W - W_0}{W + k_w} B - r_w W, \quad (2)$$

where water infiltration is modelled as a saturation function of plant biomass, characterized by the minimum proportion of rainfall infiltration in the absence of vegetation (i_0 , dimensionless), a half saturation constant (k_i , g m^{-2}) and daily precipitation (P , mm day^{-1}). Plant transpiration is controlled by plant growth, and is modulated

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by a plant-water-consumption coefficient (c , L g^{-1}). Finally, water losses to both deep drainage and direct evaporation are modeled as a linear function of soil–water availability, with a rate r_w (day^{-1}). A Maple 9.5 (Maplesoft, Waterloo, Canada) code for this model is available for download as online supporting material of this article.

Two contrasted sets of plant-growth and mortality coefficients were applied to the aforementioned model to simulate vegetation dynamics for an herbaceous species ($g_{\max} = 0.32 \text{ day}^{-1}$, $m = 0.05 \text{ day}^{-1}$) and a shrub ($g_{\max} = 0.12 \text{ day}^{-1}$, $m = 0.03 \text{ day}^{-1}$), following criteria established in previous studies (Ogle and Reynolds, 2004; Gilad et al., 2007). Plant–biomass dynamics for these two vegetation types (Fig. 1a) were modelled using a north Chihuahuan 15 year daily precipitation series obtained at the Sevilleta National Wildlife Refuge (Sevilleta LTER, <http://sev.lternet.edu/data/sev-1>; mean annual rainfall 238 mm) and a set of plausible parameters obtained from literature: $W_0 = 0.05 \text{ mm}$, $k_w = 0.45 \text{ mm}$, $k_i = 180 \text{ g m}^{-2}$, $i_0 = 0.20$, $c = 0.1 \text{ L g}^{-1}$, $r_w = 0.1 \text{ day}^{-1}$ (Rietkerk et al., 2002; Gilad et al., 2007; Saco and Moreno-de las Heras, 2013).

Using this model, we explored the strength of the plant biomass–precipitation relationship as a function of the length of rainfall accumulation (Fig. 1b). We have applied Pearson’s R correlation between the simulated plant biomass for both the herbaceous and the shrub species and antecedent precipitation series using various lengths of rainfall accumulation; i.e. for any time t_i in the plant biomass series, the precipitation in the preceding day (t_{i-1}), the cumulative precipitation in the two preceding days ($t_{i-1}; t_{i-2}$), in the three preceding days ($t_{i-1}; t_{i-2}; t_{i-3}$) and so on. The plant biomass–rainfall correlation is maximized at 52 days and 104 days of cumulative rainfall for the modeled herbaceous and shrub species, respectively (Fig. 1b). This result indicates that the simulated herbaceous species responds to short-term (\sim two months) antecedent rainfall for the production of plant biomass whilst the simulated shrub species responds to a longer period of antecedent precipitation to support plant dynamics. Further analysis using a range of plausible values for the plant-mortality and maximum plant-growth coefficients (Fig. 1c) indicates that the rainfall accumulation length (in days) of the antecedent precipitation series which maximizes the plant biomass–rainfall relationship

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(the biomass-rainfall signature of vegetation, RaL_{max}) strongly increases by reducing the characteristic plant-mortality and growth rates of vegetation, and therefore suggests a high sensitivity to vegetation type. These modelling results illustrate conceptually the distinct dependence of the relationship between plant biomass and antecedent precipitation on vegetation type, particularly when comparing the dynamics of dryland herbaceous and shrub vegetation.

In the following part of this study, we empirically define and use reference vegetation-type specific relationships between aboveground green biomass and antecedent precipitation to explore the spatial organization and NPP dynamics of herbaceous and shrub vegetation at a semi-arid grassland-shrubland ecotone, by analyzing the relationship between remotely sensed NDVI and antecedent rainfall across an area with variable abundance of herbaceous and shrub vegetation.

3 Materials and methods

3.1 Study area

This study is conducted in the Seville National Wildlife Refuge (SNWR), central New Mexico, USA, the location of the Seville Long Term Ecological Research (LTER) site. The SNWR is located in the northern edge of the Chihuahuan Desert, and is a transition zone between four major biomes: the Chihuahuan Desert, the Great Plains grasslands, the Colorado Plateau steppe, and the Mogollon coniferous woodland (Fig. 2a). Livestock grazing has been excluded from the SNWR since 1973, following 40 years of rangeland use. Due to the biome-transition nature of the SNWR, minor variations in environmental conditions and/or human use can result in large changes in vegetation composition and distribution at the refuge (Hochstrasser et al., 2002; Turnbull et al., 2010a). Of particular interest is the shrub-encroachment process that has affected the SNWR over the last century. Analysis of aerial photographs and soil-carbon isotopes indicate that the extent of desert shrublands has considerably increased over the grass-

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lands over the last 80 years despite the exclusion of cattle in the area since 1973, which suggests that other factors and mechanisms (e.g. rainfall variations, erosion-vegetation feedbacks) may have contributed to the observed vegetation change (Gosz, 1992; Turnbull et al., 2008).

Our study area is an 18 km² grassland-shrubland ecotone within the McKenzie Flats, an area of gently sloping terrain on the eastern side of the SNWR (Fig. 2b). This study area extends over two LTER core sites established in 1999 (Fig. 2c): a desert shrubland (Creosotebush SEV LTER Core Site) dominated by creosotebush, and a grassland (Black Grama SEV LTER Core Site) dominated by black grama. Broadly, the central and northeastern parts of the study area are mixed black and blue grama (*Bouteloua eriopoda* and *B. gracilis*, respectively) grasslands. The abundance of creosotebush (*Larrea tridentata*) in the grasslands is generally very low, although smaller shrubs and succulents (e.g. *Gutierrezia sarothrae*, *Ephedra torreyana*, *Yucca glauca*, *Opuntia phaeacantha*) can be common. Conversely, the abundance of perennial grass species decreases importantly to the southern and southwestern parts of the study area, where creosotebush clumps are widely distributed. Soils are Turney sandy loams (Soil Survey Staff, 2010) with about 60 % sand and 20 % silt content (Muldavin et al., 2008; Turnbull et al., 2010a). The climate is semi-arid. 1997–2013 local meteorological records indicate that mean annual precipitation is about 240 mm, with 57 % falling in the form of high-intensity convective thunderstorms during the summer monsoon (June to September) and 43 % coming in the form of low-intensity frontal rainfall and snow (October to May). Mean annual daily temperature is 14 °C, with a winter average of 6 °C and a summer average of 24 °C. Daily air temperature rises over 10 °C in the beginning of April, leading to the onset of the yearly cycles of vegetation growth (Weiss et al., 2004). Vegetation growth in the study area generally peaks between July and September, coinciding with the summer monsoon (Muldavin et al., 2008).

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3.2 Vegetation measurements (remote sensed and ground based) and rainfall data

We use temporal series of NDVI as a proxy of broad-scale aboveground green biomass dynamics in our study area. NDVI is a remote-sensed chlorophyll-sensitive vegetation index that correlates with green biomass in semi-arid environments (Anderson et al., 1993; Huete et al., 2002; Veron and Paruelo, 2010). Differences in soil background brightness can generate important uncertainties in relating NDVI levels to dryland vegetation, especially when vegetation cover is low and soil type is heterogeneous in space (Okin et al., 2001). However, multiple studies have demonstrated the usefulness of NDVI for examining primary production and vegetation structure in arid and semi-arid ecosystems (for example, Weiss et al., 2004; Choler et al., 2010; Moreno-de las Heras et al., 2012), and particularly in Chihuahuan landscapes with sparse vegetation (30–50 % cover) similar to those included in this study (Peters and Eve, 1995; Peters et al., 1997; Pennington and Collins, 2007; Notaro et al., 2010). We compiled decade-scale (2000–2013) series of NDVI with a 16 day compositing period from the MODIS Terra satellite (MOD13Q1 product, collection 5, approx. 250 m resolution). We used the NASA Reverb search tool (NASA EOSDIS, <http://reverb.echo.nasa.gov/>) to download the corresponding MODIS tiles. The data were re-projected to UTM WGS84 and further resampled to fit our 18 km² study area (335 pixels; 231.5 m pixel resolution after re-projection to UTM coordinates). To reduce inherent noise in the NDVI time series, we checked the reliability layer of the acquired MODIS products and discarded those NDVI values that did not have the highest quality flag value (less than 1 % of data). Missing values were interpolated using a second order polynomial. The NDVI time series were then filtered by applying a Savitzky-Golay smoothing algorithm, as recommended by Choler et al. (2010).

To validate the remote sensing analysis, ground information on the spatial distribution of vegetation types was recorded at a set of 27 control points distributed within the study area (Fig. 2c). The dominance of herbaceous vegetation, shrubs, perennial

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3.3 Reference NDVI-rainfall signatures of herbaceous vegetation and shrubs

Reference NDVI-rainfall signatures for herbaceous vegetation and shrubs were explored in the Black Grama and Creosotebush SEV LTER Core Sites where vegetation is dominantly herbaceous and shrub, respectively. The 2000–2013 time series of NDVI were extracted for the two core sites (averaged from five MODIS pixels in each site, covering a total of 1200 m² per site). Pearson's correlations between NDVI and antecedent precipitation series were calculated for the two sites using various lengths of rainfall accumulation (1–300 days). The NDVI-rainfall signatures for herbaceous vegetation and shrubs were determined as the length of rainfall accumulation (in days) of the antecedent precipitation series that maximized the correlations between NDVI and rainfall in the black grama- and the creosotebush-dominated core sites, respectively. This approach assumes linearity between rainfall and both NDVI values and green biomass, as it has been broadly demonstrated to occur for dryland vegetation (Evans and Geerken, 2004; Muldavin et al., 2008; Choler et al., 2010; Notaro et al., 2010; Veron and Paruelo, 2010; Moreno-de las Heras et al., 2012). Exploratory data analysis using local records of rainfall, NDVI and field NPP confirmed linearity as a reasonable assumption for the study area.

Non-dominant vegetation types can mask the NDVI-rainfall signature of dominant vegetation in mixed landscapes (Moreno-de las Heras et al., 2012). Preliminary analysis in this study revealed important mixing effects for the creosotebush-dominated core site, where quick and strong pulses of non-dominant herbs and grasses during wet years masked the shrub-specific NDVI-rainfall signature over the period of analysis. In order to avoid confounding effects (i.e. the mixing of the dominant-shrub and non-dominant herbaceous responses to precipitation) on the identification of the local NDVI-rainfall signatures, correlations between NDVI and antecedent precipitation series (of different rainfall accumulation lengths) were determined independently for each annual cycle of vegetation growth (April–March). We identified the reference signatures for herbaceous and shrub vegetation by determining the series of antecedent precip-

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itation that consistently best explained the NDVI dynamics for the Black Grama and Creosotebush Core Sites across the 2000–2013 yearly growing cycles. The reference vegetation-type characteristic antecedent rainfall series (ARain_{hv} and ARain_s for herbaceous vegetation and shrubs, respectively) that were determined in the core sites, were further used in our 18 km² ecotone to classify landscape types and to decompose local NDVI signals into greenness components for herbaceous and shrub vegetation.

3.4 Spatial distribution of vegetation types and landscape classification

We applied analysis of the relationship between local series of NDVI and the reference ARain_{hv} and ARain_s antecedent rainfall series to determine the spatial distribution of dominant vegetation and classify landscape types over our 18 km² ecotone study area. This analysis builds on the assumption that spatial variations in the NDVI-rainfall relationship reflect spatial differences in the dominance of vegetation types. We assume that areas dominated by herbaceous vegetation (or shrubs) will show a high strength on the NDVI-rainfall relationship for the herbaceous-characteristic ARain_{hv} (or the shrub-characteristic ARain_s) antecedent rainfall series along the study period. Conversely, a low strength on the NDVI-rainfall relationship consistently obtained across the 2000–2013 cycles of vegetation growth for a specific vegetation-characteristic antecedent rainfall series will locally evidence a low activity of the analyzed vegetation type for the study period.

The strength of the relationship between NDVI and rainfall (quantified using Pearson's *R* correlation between NDVI and antecedent precipitation) was calculated for every MODIS pixel in the study area using the reference ARain_{hv} and ARain_s antecedent rainfall series. Correlation values were determined independently for each cycle of vegetation growth (April–March) in 2000–2013. In order to summarize data variability from this complicated dataset (9380 correlations spatially and temporally distributed in 335 MODIS pixels and 14 growing cycles, respectively), we applied Principal Component Analysis (PCA) using the calculated correlation coefficients as variables for analysis (28 variables resulting from the two vegetation-specific antecedent rainfall series and

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the 14 growing cycles). We further studied the relationship between the main PCA factors and ground-based dominance of vegetation types using the reference vegetation distribution dataset (27 control points). Finally, we used the empirical relationships between vegetation dominance and the main PCA factors to classify the study area into four homogeneous and differentiated landscape types: grass-dominated (GD), grass-transition (GT), shrub-transition (ST) and shrub-dominated (SD) landscapes.

3.5 NDVI decomposition and transformation into herbaceous and shrub ANPP components

Time series of NDVI at any specific location reflects the additive contributions of the bare soil, herbaceous vegetation and woody shrub components (C_{bs} , C_{hv} , and C_s , respectively) for that particular site (Lu et al., 2003):

$$NDVI(t) = C_{bs}(t) + C_{hv}(t) + C_s(t), \quad (3)$$

Montandon and Small (2008) carried out in situ measurements of field spectra convolved by the MODIS bands to determine the contribution of the bare soil component to NDVI in the SNWR. They obtained a bare soil NDVI value of 0.12 for Turney sandy loam soils, which are broadly distributed across the McKenzie Flats. Preliminary analysis of the local MODIS NDVI series revealed that this soil background reference value broadly matches the minimum NDVI values for our study area. Soil background NDVI may change with soil-moisture content (Okin et al., 2001). Although this effect can be especially important for dark organic-rich soils, soil-moisture variations have shown a little impact in desert-type bright sandy and sandy-loam soils, as those represented in the study area (Huete et al., 1985). Therefore, a constant value of 0.12 was applied to subtract the bare soil component (C_{bs}) from the NDVI time series, obtaining a new set of series free of the soil background contribution ($NDVI_O$):

$$NDVI_O(t) = C_{hv}(t) + C_s(t), \quad (4)$$

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We further applied the reference herbaceous- and shrub-characteristic antecedent rainfall series, $ARain_{hv}$ and $ARain_s$, to partition single time series of soil-free NDVI ($NDVI_O$) into separate contributions for herbaceous vegetation (C_{hv}) and woody shrubs (C_s) across our study area. This approach is based on the assumption that the primary determinant of the dynamics of both NDVI and green biomass in Chihuahuan landscapes is the rainfall pattern (Huenneke et al., 2002; Weiss et al., 2004; Muldavin et al., 2008; Pennington and Collins, 2007; Notaro et al., 2010; Forzieri et al., 2011), and therefore the partial contributions of herbaceous vegetation and shrubs to NDVI can be estimated as a function of the vegetation-type characteristic use of rainfall. In other words, we assume that C_{hv} and C_s for any t_i are proportional to $ARain_{hv}$ and $ARain_s$. The NDVI components for herbaceous vegetation and shrubs were partitioned using the following two-step NDVI-decomposition procedure.

First, we applied first-order least-squares optimization of the relationship between soil-free NDVI ($NDVI_O$) and the vegetation-type specific antecedent rainfall series ($ARain_{hv}$ and $ARain_s$ for herbaceous vegetation and shrub, respectively):

$$NDVI_O(t) = hARain_{hv}(t) + sARain_s(t), \quad (5)$$

where, h and s represent vegetation-type specific rainfall-NDVI conversion coefficients for the herbaceous and shrub components.

Secondly, we used the determined coefficients h and s to calculate the weights of C_{hv} and C_s on the time series (i.e. the predicted percentage contribution of each vegetation type over the predicted totals for any t_i). Seasonal variations in other environmental factors (e.g. temperature, day length) may influence NDVI dynamics for Chihuahuan vegetation, shaping the responses of vegetation to precipitation (Weiss et al., 2004; Notaro et al., 2010). In order to preserve the observed seasonality of the original NDVI time series in the decomposed signals for herbaceous and shrub vegetation, the predicted weights (or percentage contributions) of the fitted vegetation components were reassigned to the NDVI levels of the original time series, obtaining the final NDVI components for herbaceous vegetation and shrubs (C_{hv} , and C_s , respectively).

Explorative comparisons revealed that this simple two-step procedure outperformed other more complex NDVI-decomposition methodologies (e.g. artificial neural network, autoregressive and non-linear modeling). In order to facilitate the application of this NDVI-decomposition procedure by other users, the Maple 9.5 (Maplesoft, Waterloo, Canada) code that we developed is available for download as online supporting material of this article.

The overall 2000–2013 time series of NDVI were decomposed into separate contributions of herbaceous vegetation and shrubs for the Black Grama and Cresotebush SEV LTER Core Sites. We used the reference 2000–2011 field NPP dataset to study the relationship between the decomposed NDVI time series and ground-based estimates of herbaceous and shrub NPP for the core sites. The sum of the herbaceous and the shrub NDVI components ($\sum \text{NDVI}_{\text{veg.type}}$) were calculated for each growing cycle of vegetation (April–March). We further determined the relationships between field ANPP estimates of herbaceous and shrub vegetation and $\sum \text{NDVI}_{\text{veg.type}}$. Finally, we applied the signal-decomposition procedure to every single NDVI time series of the 335 MODIS pixels contained within our study area. The established core site NDVI-ANPP relationships were used to estimate herbaceous and shrub ANPP across the 18 km² study site.

3.6 Impact of seasonal precipitation on herbaceous and shrub ANPP

We used the remotely sensed ANPP estimations and landscape-type classification (GD, grass-dominated, GT, grass-transition, ST, shrub-transition, and SD, shrub-dominated landscapes) to analyze the impact of inter-annual variations in seasonal precipitation on the production of herbaceous and shrub vegetation at our study grassland-shrubland ecotone. Three different seasonal precipitation metrics were used in this analysis: (i) preceding non-monsoonal rainfall (Rain_{PNM} , from October to May) that takes place before the summer peak of vegetation growth, (ii) summer monsoonal precipitation (Rain_{SM} , from June to September), and (iii) late non-monsoonal rainfall

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($Rain_{LNM}$, from October to March) that takes place at the end of the annual cycles of vegetation growth.

We explored the effects of seasonal precipitation on herbaceous and shrub ANPP for the established landscape types (grass-dominated, grass-transition, shrub-transition and shrub-dominated landscapes) by applying Pearson's R correlation. Effect significance and size was further determined using a general linear model (GLM) that includes the different sources of seasonal precipitation ($Rain_{PNM}$, $Rain_{SM}$, and $Rain_{LNM}$) as covariates, landscape type (LT) as a factor, and the interaction terms between landscape type and seasonal precipitation ($LT : Rain_{PNM}$, $LT : Rain_{SM}$, and $LT : Rain_{LNM}$).

4 Results

4.1 Patterns of greenness and reference NDVI-rainfall signatures in the core sites

Inter- and intra-annual variations of NDVI show similar patterns of vegetation greenness for both the Black Grama and the Creosotebush Core Sites (Fig. 3a). The signal generally peaks slightly in spring (May) and strongly in summer (July–September). Similarly, the lowest NDVI values are reached between February and April. Summer peaks in NDVI values are, however, less intense in the Creosotebush Core Site. In addition, the NDVI signal for the creosotebush-dominated site generally shows an autumn (October–November) peak that is especially important during particular growing cycles (2000–2001, 2001–2002, 2004–2005, 2007–2008, 2009–2010).

Correlations between NDVI and antecedent precipitation using various rainfall accumulation periods indicate that a short-term cumulative rainfall period of nearly 57 days best explains the NDVI variations for the dominant herbaceous vegetation of the grassland site for all the annual cycles of vegetation growth (Fig. 3b, see also Fig. S1 in the Supplement for this study). For the Creosotebush Core Site (with dominant shrub vegetation and subordinated forbs and grasses), the short-term, 57 days antecedent

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rainfall series also has an important impact on the strength of the NDVI-rainfall relationship, particularly for three consecutive growing cycles with strong summer precipitation (2006–2007, 2007–2008 and 2008–2009, summer precipitation for the period is 40 % above the long-term mean). However, the NDVI-rainfall correlation in this shrub-dominated site generally peaks using a much longer cumulative rainfall period of nearly 145 days.

4.2 Spatial distribution of vegetation types and landscape classification

Figure 4a and b displays the main PCA results derived from the spatial analysis of the NDVI-rainfall correlation coefficients (per growing cycle) for the reference 57 and 145 day antecedent rainfall series (i.e. ARain_{hv} and ARain_s, respectively) in all MODIS pixels contained within our study area. PCA factor 1 (about 40 % of total data variance) reflects a landscape gradient that discriminates the two reference NDVI-rainfall signatures. The correlation between the NDVI and the short-term antecedent rainfall series (57 days) increases to the negative side of factor 1 (particularly for growing cycles 2001–2002, 2002–2003, 2005–2006, and 2012–2013), while the correlation with the 145 day antecedent rainfall series increases to the positive side of this factor (particularly for cycles 2000–2001, 2002–2003, 2005–2006, and 2006–2007, Fig. 4b). Analysis of the relationship between PCA factor 1 and vegetation dominance for the ground-based set of control points indicates that this landscape gradient is explained by the field distribution of dominant vegetation types since the dominance of herbaceous vegetation and shrubs increases to the negative and positive side of PCA factor 1, respectively (Fig. 4c).

Four different landscape types (GD, GT, ST and SD) are defined in the 18 km² study area as determined by the spatial projection of the relationship between PCA factor 1 and field dominance of herbaceous and shrub vegetation (Fig. 4c and d). SD, ST and GT landscapes are distributed in the southwestern part of the study site, while GD landscapes are located in the central and northeastern parts of the area (Fig. 4d and e).

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4.3 NDVI transformation into herbaceous and shrub ANPP components

Temporal decomposition of NDVI into partial herbaceous and shrub vegetation components results in very different outputs for the reference Black Grama and Creosotebush Core sites (Fig. 5a). The herbaceous component (which is derived from the relationship between NDVI and the reference 57 day antecedent rainfall series, $ARain_{hv}$) clearly prevails in the grass-dominated reference site. Conversely, the shrub component (which is function of the reference 145 day antecedent rainfall series, $ARain_s$) comprises the leading NDVI fraction in the shrub-dominated reference site. In addition, the (per growing cycle) annual sums of herbaceous and shrub NDVI components for the reference sites show a good and strong linear agreement ($R^2 \geq 0.65$; $P < 0.001$) with ground-based estimations of ANPP (Fig. 5b).

Spatial projection of the reference NDVI-ANPP relationships across the 18 km² study area displays a contrasted distribution of mean 2000–2013 ANPP for herbaceous and shrub vegetation (Fig. 5c and d). Herbaceous ANPP is mainly distributed in the central and northeastern parts of the study site. Conversely, shrub ANPP is concentrated in the southwestern edge of the study area (Fig. 5d).

4.4 Impact of seasonal precipitation on herbaceous and shrub primary production

Exploratory analysis of the influence of seasonal precipitation on remote-sensed estimations of ANPP indicates variable responses for herbaceous and shrub vegetation (Fig. 6). Herbaceous ANPP strongly correlates with monsoonal summer precipitation for all landscape types (Fig. 6a). The slope of the relationship between herbaceous ANPP and monsoonal summer (June–September) precipitation decreases for the shrub-transition and shrub-dominated landscapes. On the other hand, shrub ANPP strongly correlates with both preceding non-monsoonal (October–May) and monsoonal summer (June–September) precipitation for all landscape types (Fig. 6b).

The analysis of the relationships between NDVI and precipitation provide further insights on plant water-use patterns and, hence, on vegetation function and structure (Pennington and Collins, 2007; Veron and Paruelo, 2010; Notaro et al., 2010; Garcia et al., 2010; Forzieri et al., 2011; Moreno-de las Heras et al., 2012). Temporal trends in NDVI for the reference grass- and shrub-dominated SEV LTER sites are explained by antecedent (or preceding cumulative) rainfall amounts, reflecting the coupling of the history of plant-available soil moisture with vegetation growth (Fig. 3b). Correlations between NDVI and precipitation indicate that plant growth pulses for the grass-dominated site are associated with short-term (57 days) antecedent rainfall. For the shrub-dominated landscape, leaf phenology shows a strong association with medium-term (145 days) antecedent precipitation, although importantly, NDVI dynamics for this site also correlate with the 57 day cumulative rainfall series. Previous work on the analysis of NDVI-rainfall relationships found similar variations in the length of the antecedent rainfall series that best explain the dynamics of vegetation greenness, suggesting that such differences result from site variations in dominant vegetation (Evans and Geerken, 2004; Prasad et al., 2007; Garcia et al., 2010).

Our modeling results provide a biophysical explanation for the range of variations found in the NDVI-rainfall relationships (Fig. 1). The length of the cumulative precipitation series that maximizes the relationship between plant biomass and antecedent rainfall appears to be a function of the characteristic water-use and plant growth pattern of dryland vegetation, that are ultimately controlled by the plant-growth and mortality rates of vegetation (Fig. 1c). Vegetation growth and water use strongly differ for herbaceous and shrub life-forms in drylands (Sparrow, 1997; Ogle and Reynolds, 2004; Gilad et al., 2007; Garcia et al., 2010), in which case plant biomass dynamics respond to short-term and long-term antecedent precipitation, respectively (Fig. 1a and b). Variations in NDVI-rainfall signatures (i.e. the rainfall accumulation length of the antecedent precipitation series that best explain the NDVI dynamics) in the reference SEV LTER core sites may, therefore, be expressed as a function of the dominant vegetation types (Fig. 3): the strong and quick responses of greenness to short-term precipitation (reference

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57 day antecedent rainfall series, $ARain_{hv}$) in the grass-dominated Black Grama Core Site characterize the NDVI-rainfall signature of herbaceous vegetation for the area, while the slow responses of NDVI to medium-term precipitation (reference 145 day antecedent rainfall series, $ARain_s$) in the shrub-dominated Cresotebush Core Site define the characteristic shrub signature. The high correlation between the short-term (57 days) antecedent rainfall series and NDVI values in the shrub-dominated Creosotebush Core Site (Fig. 3b) could be explained by the growth of non-dominant herbaceous vegetation (mainly forbs), which can be especially important during wet years (Muldavin et al., 2008; Baez et al., 2012). Overall, the length of the reference NDVI-rainfall signatures determined for herbaceous and shrub vegetation in this work are in agreement with the range of characteristic antecedent rainfall series reported in other studies to best describe green biomass dynamics for arid and semi-arid grasslands (1–2 months) and woody shrublands (4–8 months) (Evans and Geerken, 2004; Munkhtsetseg et al., 2007; Garcia et al., 2010; Moreno-de las Heras et al., 2012).

5.2 Spatial distribution and net primary production of herbaceous vegetation and shrubs

Our results indicate that the relationship between temporal series of remotely sensed NDVI and antecedent precipitation is highly sensitive to spatial differences in dominant vegetation (Fig. 4). In fact, the main PCA factor (about 40 % variability in data) extracted using the annual NDVI responses (i.e. the Pearson's R coefficients) to the reference 57 and 145 day characteristic antecedent rainfall series ($ARain_{hv}$ and $ARain_s$ series, respectively) accurately discriminates the behavior of herbaceous and shrub vegetation for the 18 km² study area (Fig. 4b and c), hence providing a robust approach for classifying landscapes as a function of the dominance of vegetation types using coarse-grained remotely sensed data (Fig. 4d). This parsimonious approach offers a practical alternative to other more complex remote-sensing methodologies for the analysis of the spatial distribution of vegetation types in mixed systems, such as Spectral Mixture Analysis (SMA, Smith et al., 1990), which may be difficult to apply in

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this Chihuahuan case study since both the mixed nature and fine-grained distribution of vegetation in the area (patches of grass and shrubs are typically $< 1 \text{ m}^2$ and $0.5\text{--}5 \text{ m}^2$, respectively; Turnbull et al., 2010a) can impose serious drawbacks on the detection of reference spectral signatures for pure herbaceous and shrub vegetation using coarse-grained MODIS data. In fact, implementing SMA-based approaches for the analysis of vegetation distribution and landscape classification in drylands using medium- and coarse-grained data is very challenging since it requires significant amounts of ancillary data (e.g. lab-based or field multi-date spectra for vegetation types) to solve data uncertainties generated by surface heterogeneity, which is often not feasible (Somers et al., 2011).

The relationships of vegetation greenness to the reference herbaceous- and shrub-characteristic antecedent rainfall series (ARain_{hv} and ARain_{s}) also provide criteria for decomposing and transforming the NDVI signal into structural components of primary production for this study. Lu et al. (2003) applied seasonal trend decomposition to partition NDVI into (cyclic) herbaceous and (trend) woody vegetation in Australia. They assumed a long-term weak phenological wave and a strong annual response for determining the shrub and herbaceous components of vegetation, respectively. Our approach relies on the use of differences in biophysical properties of herbaceous and shrub vegetation related to the coupling between vegetation growth and precipitation for decomposing the NDVI signal, rather than apparent differences in the seasonality of vegetation greenness alone. As expected, signal decomposition outcomes indicate that the herbaceous component of the NDVI leads the temporal trends for the grass-dominated reference Black Grama Core Site, while the shrub component largely dominates the NDVI signal for the Creosotebush Core Site (Fig. 5a). Although affected by data dispersion, the annual sums of decomposed NDVI strongly agree with field estimations of ANPP for herbaceous and shrub vegetation (Fig. 5b). In addition, the spatial organization of the remote-sensed estimations of herbaceous and shrub ANPP matches the observed distribution of dominant vegetation types (Figs. 4c and d and 5c and d). Other dryland studies have found important levels of data dispersion when

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relating fine-grained field ANPP to coarse-scale NDVI values (Lu et al., 2003; Holm et al., 2003; Pennington and Collins, 2007; Veron and Paruelo, 2010). Major sources of data dispersion for this study are most likely associated with the high spatial variability of ANPP in the analyzed systems. For instance, field estimations have shown that ANPP for both grass- and shrub-dominated Chihuahuan landscapes are affected by important levels of spatial variability, primarily due to the patchiness of vegetation cover (Huenneke et al., 2002; Muldavin et al., 2008).

5.3 Impact of variations in seasonal precipitation on herbaceous and shrub primary production

Cross-scale interactions between climatic drivers (e.g. variations in precipitation amount and seasonality), vegetation composition and individual plant characteristics have an important role on determining primary production patterns in arid and semi-arid ecosystems (Peters, 2002; Snyder and Tartowsky, 2006; Pennington and Collins, 2007; Notaro et al., 2010; Baez et al., 2013). Results of our remote sensing estimations of ANPP for dominant vegetation types indicate that primary production is differently controlled by seasonal precipitation for herbaceous and shrub vegetation across the 18 km² Chihuahuan Desert ecotone (Fig. 6, Table 1). Monsoonal summer precipitation (June–September) controls ANPP for herbaceous vegetation (Fig. 6a), while ANPP for shrubs is better explained by the preceding year's non-monsoonal (October–May) plus the summer monsoonal precipitation in the present year (Fig. 6b). Accordingly, field observations of ANPP for Chihuahuan landscapes found that grassland primary production is particularly coupled with monsoonal rainfall, while desert shrublands appear to be less dependent on summer precipitation (Fisher et al., 1988; Reynolds et al., 1999; Huenneke et al., 2002; Muldavin et al., 2008; Throop et al., 2012).

Differences in the distribution of rainfall types, soil-moisture dynamics, and rooting habits of dominant plant species may explain the variable impact of seasonal precipitation on herbaceous and shrub ANPP for the studied Chihuahuan landscapes. Monsoonal summer precipitation (July–September, approx. 60 % annual precipitation) gen-

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erally takes place in the form of high-intensity thunderstorms that infiltrate shallow soil depths (top 15–35 cm) (Snyder and Tartowsky, 2006). Summer soil–water resources for plant production are ephemeral and strongly affected by evapotranspiration, which typically reduces soil moisture to pre-storm background levels in 4–7 days after rain-
 5 fall (Turnbull et al., 2010b). *C*₄ grasses (*Bouteloua eriopoda* and *B. gracilis*), which dominate herbaceous vegetation in the analyzed ecotone, concentrate active roots in the top 30 cm of the soil and intensively exploit ephemeral summer soil moisture for plant growth (Peters, 2002; Muldavin et al., 2008). Preferential spatial redistribution of runoff to grass patches following summer storms further enhances plant production for
 10 black and blue grama (Wainwright et al., 2000; Pockman and Small, 2010; Turnbull et al., 2010b). Conversely, non-monsoonal precipitation (about 40 % annual precipitation, primarily from November to February) typically falls in the form of long-duration low-intensity frontal rainfall that often percolates to deep soil layers (Snyder and Tar-
 15 towsky, 2006). *Larrea tridentata*, the dominant *C*₃ shrub in the studied ecotone, has a bimodal rooting behavior that facilitates the use of both shallow and deep soil moisture for plant production (Fisher et al., 1988; Reynolds et al., 1999; Ogle and Reynolds, 2004). Deep creosotebush roots (70–150 cm depth) may acquire winter-derived soil–water resources that are unavailable to grass species, while active roots near the sur-
 20 face (20–40 cm depth) may serve to access summer-derived shallow soil moisture for plant growth (Gibbens and Lenz, 2001). The observed reduction in summer rain-use efficiency of herbaceous vegetation for the shrub-transition and shrub-dominated land-
 25 scapes (i.e. variations on the slope of the relationship between herbaceous ANPP and summer precipitation, Fig. 6a) suggests competitive effects of creosotebush for the use of shallow water sources, probably associated to the large spatial extent of near-surface active roots (the radial spread of which typically ranges between 2–6 m, Gibbens and Lenz, 2001). Alternative, landscape changes induced by shrub encroachment (i.e. in-
 creased runoff and erosion) may reduce the ability of grass patches to capitalize on horizontal redistribution of runoff for plant growth after summer storms (Wainwright et al., 2000; Turnbull et al., 2012; Stewart et al., 2014).

Conceptual and mechanistic models of vegetation change suggest that vegetation composition in arid and semi-arid landscapes is likely to be highly sensitive to climate change, and point at variations in the amount and distribution of precipitation as a major driver of shrub encroachment into desert grasslands (Peters, 2002; Gao and Reynolds, 2003; Snyder and Tartowsky, 2006). Overall our results agree with those findings and suggest that changes in the amount and temporal pattern of precipitation comprising reductions in monsoonal summer rainfall and/or increases in winter precipitation may enhance the encroachment of creosotebush into desert grasslands dominated by black and blue grama. Analysis of long-term rainfall series indicates that winter precipitation has increased during the past century in the northern Chihuahuan Desert, particularly since 1950, probably associated with the more frequent occurrence of ENSO events for that period (Wainwright, 2006). This pattern of precipitation change may be responsible, at least in part, of the recent increase in woody shrub abundance over desert grasslands in the American Southwest (Brown et al., 1997; Snyder and Tartowsky, 2006; Webb et al., 2003). Climate-change projections for the area suggest a general picture of increased aridity, with increased evaporation due to higher summer temperatures, and increased drought frequency (Christensen and Konikicharla, 2013). The capacity of *L. tridentata* to switch between different soil–water sources (i.e. summer-derived ephemeral shallow soil moisture and more stable deep soil–water reserves derived from winter rainfall) and adapt the timing of vegetation growth to take advantage of changes in resource availability make this C_3 shrub less susceptible to predicted increases in aridity than C_4 grasses that are strongly dependent on summer precipitation (Reynolds et al., 1999; Throop et al., 2012; Baez et al., 2013). Current increases in atmospheric CO_2 concentrations may also contribute to reduce the competitiveness of C_4 grasses for the use of soil–water resources against C_3 desert shrubs (Polley et al., 2002). Remaining desert grasslands in the American Southwest may, therefore, be increasingly susceptible to shrub encroachment under the present context of changes in climate and human activities.

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6 Conclusions

In this study we applied a new methodology of analysis for the study of the organization and dynamics of vegetation at a grassland-shrubland Chihuahuan ecotone with variable abundance of grasses (primarily *Bouteloua eriopoda* and *B. gracilis*) and shrubs (mainly *Larrea tridentata*), based on the exploration of the relationship between time series of remote-sensed vegetation greenness (NDVI) and precipitation. Our results indicate that the characteristics of the NDVI-rainfall relationships are highly dependent on differences in water-use and plant growth pattern of vegetation types. In fact, NDVI-rainfall relationships show a high sensitivity to spatial variations on dominant vegetation types across the grassland-shrubland ecotone, and provide ready biophysically based criteria to study the spatial distribution and dynamics of net primary production (NPP) for herbaceous and shrub vegetation. The analysis of the relationship between NDVI and precipitation offers, therefore, a powerful methodology for the study of broad-scale ecotone dynamics and vegetation shifts comprising large changes in the dominance of vegetation types in drylands using coarse-grained remotely sensed data, and could be used to target areas for more detailed analysis and/or the application of mitigation measures.

Analysis of remote-sensed NPP dynamics at the grassland-shrubland ecotone reflects a variable performance of dominant vegetation types. Herbaceous production is synchronized with monsoonal summer rainfall, while shrub NPP shows a flexible response to both summer and winter precipitation. Overall our results suggest that changes in the amount and temporal pattern of precipitation (i.e. reductions in summer precipitation and/or increases in winter rainfall) may intensify the shrub-encroachment process in the studied desert grasslands of the American Southwest, particularly in the face of predicted general increases in aridity and drought frequency for the area.

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Table 1. Main effects and interactions of seasonal precipitation (preceding non-monsoonal rainfall, October–May; monsoonal summer rainfall, June–September; late non-monsoonal rainfall, October–March) and landscape type (4 levels: grass-dominated, grass-transition, shrub-transition, and shrub-dominated landscapes) on remote-sensing estimated annual (per growing cycle, April–March) net primary production for herbaceous vegetation and shrubs.

	<i>F</i>	df	<i>P</i>	η^2 (%)
Herbaceous vegetation ANPP _{r.sensing}				
Rain _{PNM} (Oct–May)	194.2	1	0.000	4.2
Rain _{SM} (Jun–Sep)	1483.4	1	0.000	25.4
Rain _{LNM} (Oct–Mar)	129.3	1	0.000	2.0
LT	35.9	3	0.000	2.3
LT : Rain _{PNM} (Oct–May)	122.4	3	0.000	7.8
LT : Rain _{SM} (Jun–Sep)	282.4	3	0.000	16.2
LT : Rain _{LNM} (Oct–Mar)	1.1	3	0.326	0.0
Shrubs ANPP _{r.sensing}				
Rain _{PNM} (Oct–May)	1661.2	1	0.000	27.7
Rain _{SM} (Jun–Sep)	1720.8	1	0.000	28.4
Rain _{LNM} (Oct–Mar)	7.1	1	0.010	0.1
LT	2.9	3	0.030	0.2
LT : Rain _{PNM} (Oct–May)	6.6	3	0.000	0.4
LT : Rain _{SM} (Jun–Sep)	46.2	3	0.000	3.0
LT : Rain _{LNM} (Oct–Mar)	31.9	3	0.000	2.1

Abbreviations: ANPP_{r.sensing}, remote-sensed annual net primary production; Rain_{PNM} (October–May), preceding non-monsoonal rainfall; Rain_{SM} (June–September), monsoonal summer rainfall;

Rain_{LNM} (October–March), late non-monsoonal rainfall; LT, landscape type; ‘:’, interaction terms; η^2 , eta-squared (effect size).

Notes: η^2 values in bold are > 10 % (effects that contribute in more than 10 % to the total variance comprised in ANPP_{r.sensing}).

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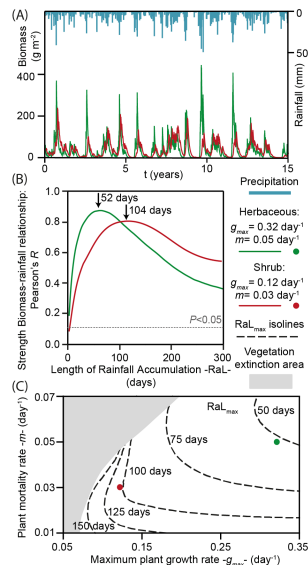


Figure 1. Simulated dryland biomass–rainfall relationships for herbaceous and shrub vegetation: **(a)** modelled biomass dynamics for an herbaceous (green) and a shrub (red) species, **(b)** strength of the biomass–precipitation relationship (Pearson's R correlation) using different lengths of rainfall accumulation (RaL) for the simulated herbaceous and shrub species (values above the dotted grey line are significant at $P < 0.05$), **(c)** plant biomass–rainfall signature (RaL_{max} , length of rainfall accumulation that maximizes the plant biomass–precipitation relationship) as a function of the plant-growth and mortality rates. The green and red dots in panel **(c)** indicate RaL_{max} values obtained for the simulated herbaceous (52 days) and shrub (104 days) species, respectively. The (grey) “vegetation extinction” area in panel **(c)** reflects combined values of plant-growth and mortality rates that do not support long-term vegetation dynamics for the simulated rainfall conditions.

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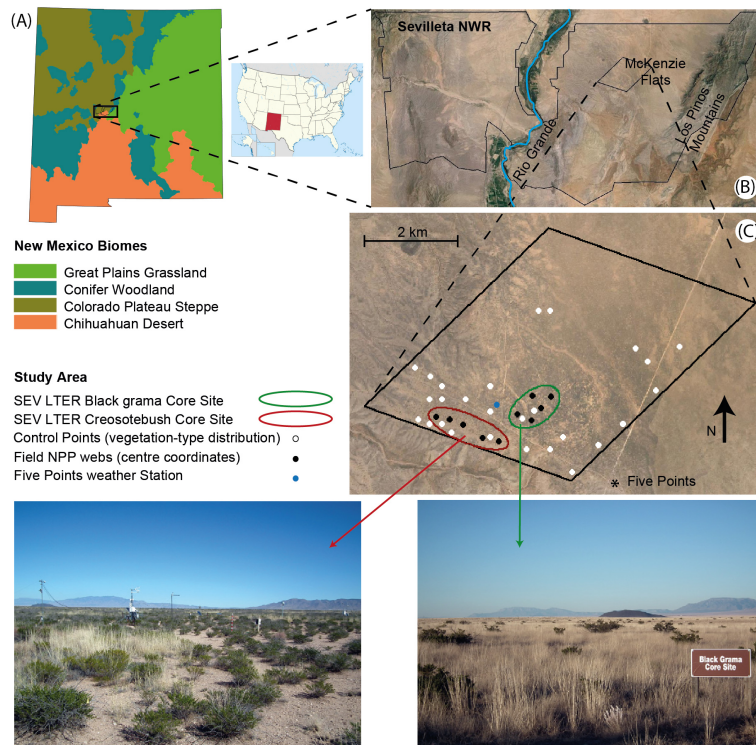


Figure 2. Study area: **(a)** location of the Seville National Wildlife Refuge (SNWR) and distribution of major New Mexico biomes, **(b)** regional location of the study area (McKenzie Flats, SNWR), **(c)** detailed location of the study site (18 km² area) and general view of the reference SEV LTER Black Grama (right) and Creosotebush (left) Core Sites. Map **(a)** follows the Seville LTER classification of New Mexico biomes (Seville LTER, <http://sev.lternet.edu/content/new-mexico-biomes-created-sevilter>). Source for background image in panels **(b)** and **(c)**: 2009 National Aerial Imagery Program (USDA Farm Service Agency).

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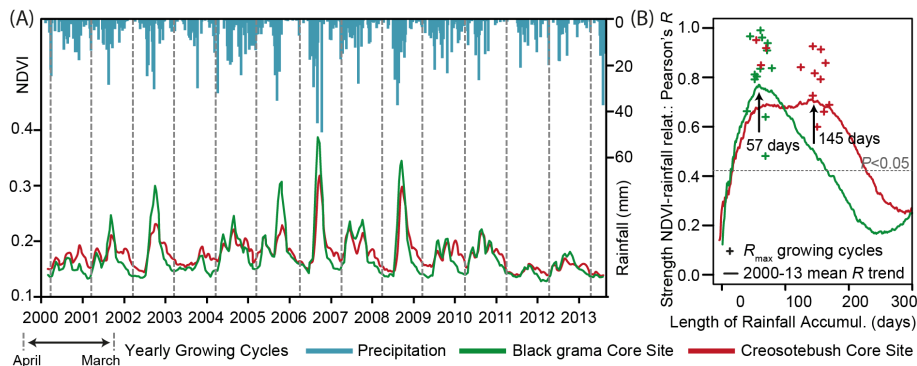


Figure 3. Reference NDVI-rainfall relationships at the SEV LTER Black Grama and Creosote-bush Core Sites: **(a)** 2000–2013 MODIS NDVI time series for the core sites, **(b)** strength of the NDVI-rainfall relationship (Pearson’s R correlation) for the core sites using different lengths of rainfall accumulation (maximum correlations, R_{\max} , for the individual growing cycles are shown together with the mean trend for 2000–2013; detailed correlograms for each growing cycle can be found in Fig. S1 in the Supplement as online supporting information for this study). R values above the dotted grey line are significant at $P < 0.05$. The arrows in panel **(b)** indicate the reference NDVI-rainfall signatures (rainfall accumulation length of the antecedent rainfall series that maximize the relationships between NDVI and precipitation) for herbaceous vegetation (57 days) and shrubs (145 days).

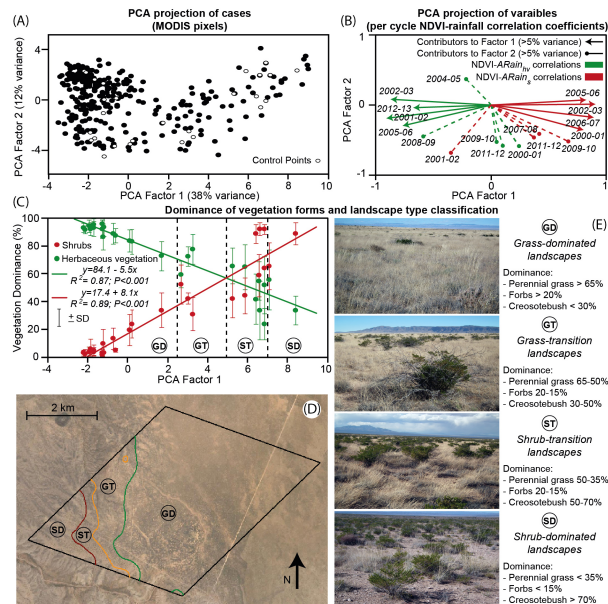


Figure 4. Principal Component Analysis (PCA) of the NDVI-rainfall correlation coefficients for the herbaceous- and shrub-specific antecedent rainfall series $ARain_{hv}$ and $ARain_s$ (57 and 145 day cumulative rainfall series, respectively) and resulting landscape type classification across the 18 km² study area: **(a)** PCA projection of cases (MODIS pixels), **(b)** PCA projection of variables (per growing cycle NDVI-antecedent rainfall correlation scores), **(c)** landscape type classification (GD, grass-dominated, GT, grass-transition, ST, shrub-transition, and SD, shrub-dominated landscapes) as a function of the relationship between PCA Factor 1 and field-estimated vegetation dominance for a reference set of 27 control points, **(d)** spatial distribution of landscape types in the study area, **(e)** general view and characteristics of the landscape types. MODIS pixel locations for the ground control points are highlighted in panel **(a)**. Vector labels in panel **(b)** indicate the dates of the yearly cycles of vegetation growth (April–March). Source for background image in panel **(d)**: 2009 National Aerial Imagery Program (USDA Farm Service Agency).

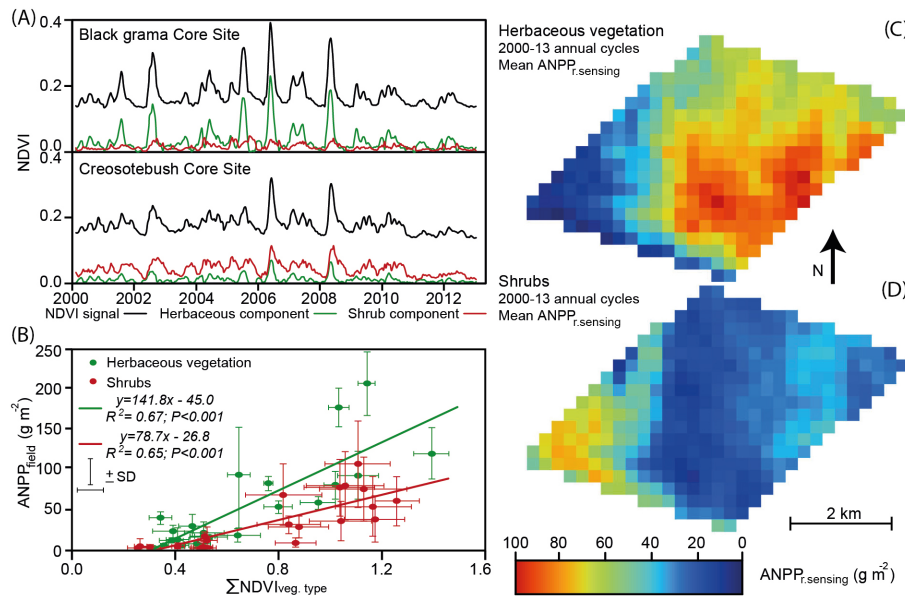


Figure 5. NDVI decomposition and transformation into partial Annual Net Primary Production (ANPP) components for herbaceous and shrub vegetation: **(a)** decomposed NDVI time series of herbaceous and shrub vegetation for the reference SEV LTER Black Grama and Creosotebush Core Sites, **(b)** relationships between field ANPP and the (per growing cycle) annual integrals of herbaceous and shrub NDVI components for the SEV LTER core sites, **(c, d)** remote-sensed ANPP estimations of herbaceous and shrub vegetation (mean for the 2000–2013 series) across the 18 km² study area.

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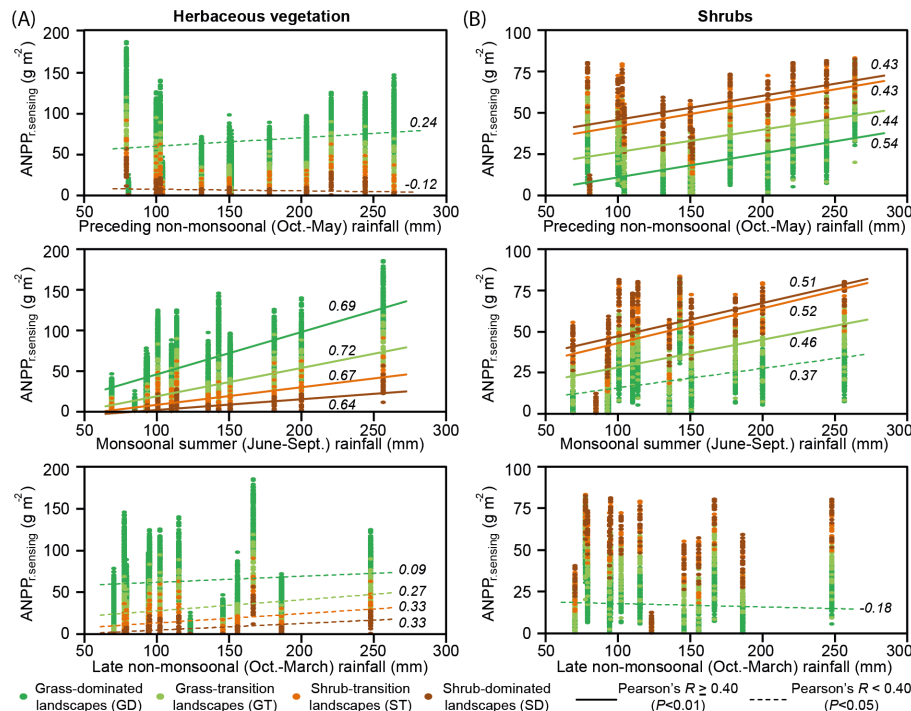


Figure 6. Scatter plots and correlations (Pearson's R) between remote-sensed ANPP estimations and seasonal precipitation (preceding non-monsoonal, summer monsoonal, and late non-monsoonal rainfall) for the different landscape types (grass-dominated, grass-transition, shrub-transition, and shrub-dominated landscapes): **(a)** herbaceous ANPP, **(b)** shrub ANPP. Solid and dotted lines represent strong ($R \geq 0.40$, $P < 0.01$) and weak ($R < 0.40$, $P < 0.05$) correlations, respectively. Numbers within the plots indicate correlation coefficients.